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BULLETIN  
OF THE  
TORREY BOTANICAL CLUB

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JUNE, 1913

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Four hybrids of *Viola pedatifida*

EZRA BRAINERD

(WITH PLATES 15-17)

The hybrids between *Viola pedatifida* and allied species are in several respects the most interesting among the 75 or 80 that have appeared in the genus as represented in North America. At least two of the four are remarkably hardy, almost immune from attacks of fungus, and comparatively fertile; they are therefore well suited for experimental cultures. The marked contrast in leaf outline displayed in the parents of the several crosses affords a fine opportunity for studying in detail the many diverse forms of leaf that emerge in the offspring of the hybrid. The other opposed parental characters, relating to pubescence, color of capsule, color of seed, length of peduncle, and villosity of spur petal, also lead to results well worthy of careful study.

One of these hybrid plants I have had in hand for eight seasons and have raised from it over 450 offspring, extending through four generations. It was discovered at Yorkville, Ill., May 1905, by Miss Mary O. Pollard, a former pupil, and may be briefly described as follows:

1. *Viola papilionacea* × *pedatifida* hyb. nov.

Rootstock stout, at length extensively branching horizontally; leaves broadly deltoid-ovate in outline, cleft into 7-11 linear or oblong lobes, the middle lobe much the widest, glabrous, though the margins are often scabro-ciliolate; petals violet, the odd one more or less villous; cleistogamous flowers on erect or ascending peduncles, intermediate in length to those of the parent species; capsules 8-12 mm. long, infertile, averaging in 12 capsules  $8\frac{1}{4}$

seeds; seeds brown, 2 mm. long; offspring notably diversiform. (PLATE 15, *Aa*.)

Several sowings have been made of the seeds of this hybrid; but the ten plants of the first brood (236), whose offspring have been raised for two succeeding generations, are the only ones that will be here discussed. The forms of leaf found in the ten plants and in their respective broods of offspring are presented in the first half of TABLE I. The second half presents the corresponding facts regarding sixteen offspring of brood 236, plant 3, whose leaf had a hybrid form, quite the same as that of the mother plant from Illinois.

TABLE I  
CULTURES OF VIOLA PAPILIONACEA X PEDATIFIDA FOR FOUR GENERATIONS

| <i>V. papilionacea</i> has leaf uncut:— <i>a</i><br><i>V. pedatifida</i> has leaf parted:— <i>A</i><br>Their HYBRID has leaf cleft:— <i>Aa</i> |              |                                |                 |           |          |          | Sixteen F <sub>3</sub> offspring of 236-3 |              |                 |          |    |       |  |
|--|--------------|--------------------------------|-----------------|-----------|----------|----------|---|--------------|-----------------|----------|----|-------|--|
| Ten F <sub>2</sub> offspring of hybrid   |              |                                |                 |           |          |          | Their offspring—F <sub>4</sub>            |              |                 |          |    |       |  |
| Brood<br>236   | Leaf<br>form | Their offspring—F <sub>3</sub> |                 |           |          |          | Brood                                     | Leaf<br>form | Number and form |          |    | Total |  |
|  |              | Brood                          | Number and form |           |          | <i>A</i> |   |              | <i>Aa</i>       | <i>a</i> |    |       |  |
|  |              |                                | <i>A</i>        | <i>Aa</i> | <i>a</i> |          |   |              |                 |          |    |       |  |
| No. 2  | <i>A</i>     | 595                            | 30              |           |          |          | No. 1                                     | <i>A</i>     | 605             | 12       |    | 12    |  |
| No. 3  | <i>Aa</i>    | 468                            | 6               | 5         | 5        | }        | No. 2                                     | <i>Aa</i>    | 606             | 3        | 5  | 13    |  |
|  |              | 596                            | 8               | 20        | 8        |          | No. 3                                     | <i>Aa</i>    | 607             | 4        | 6  | 13    |  |
| No. 4  | <i>Aa</i>    | 597                            | 3               | 6         | 1        |          | No. 4                                     | <i>A</i>     | 608             | 14       |    | 14    |  |
| No. 6  | <i>a</i>     | 598                            |                 |           | 16       |          | No. 5                                     | <i>a</i>     | 609             |          | 15 | 15    |  |
| No. 7  | <i>A</i>     | 599                            | 16              |           |          |          | No. 6                                     | <i>A</i>     | 610             | 20       |    | 20    |  |
| No. 8  | <i>Aa</i>    | 600                            | 1               | 10        | 3        |          | No. 7                                     | <i>a</i>     | 611             |          | 11 | 11    |  |
| No. 9  | <i>Aa</i>    | 601                            | 2               | 1         | 1        |          | No. 8                                     | <i>A</i>     | 612             | 14       |    | 14    |  |
| No. 10   | <i>Aa</i>    | 602                            | 6               | 6         | 3        |          | No. 9                                     | <i>a</i>     | 613             |          | 16 | 16    |  |
| No. 11   | <i>A</i>     | 603                            | 13              |           |          |          | No. 11                                    | <i>Aa</i>    | 615             | 3        | 6  | 12    |  |
| No. 12   | <i>Aa</i>    | 604                            | 3               | 5         | 2        |          | No. 12                                    | <i>Aa</i>    | 616             | 3        | 7  | 13    |  |
| Total . . . . .  |              | 88                             | 53              | 39        | 180      |          | No. 13                                    | <i>A</i>     | 617             | 12       |    | 12    |  |
| From <i>Aa</i> 's . . .  |              | 29                             | 53              | 23        | 105      |          | No. 14                                    | <i>A</i>     | 618             | 12       |    | 12    |  |
|  |              |                                |                 |           |          |          | No. 15                                    | <i>a</i>     | 619             |          | 12 | 12    |  |
|  |              |                                |                 |           |          |          | No. 16                                    | <i>Aa</i>    | 620             | 2        | 7  | 13    |  |
|  |              |                                |                 |           |          |          | No. 17                                    | <i>a</i>     | 621             |          | 14 | 14    |  |
|  |              |                                |                 |           |          |          | Total . . . . .                           |              | 99              | 31       | 86 | 216   |  |
|  |              |                                |                 |           |          |          | From <i>Aa</i> 's . . .                   |              | 15              | 31       | 18 | 64    |  |

The cultures show that in this hybrid the Mendelian law controls in a general way the inheritance of leaf form, though there is no dominance, the hybrid leaf being intermediate between the leaves of the two parents. The plants that resemble *V. pedatifida* in having parted leaves always produce offspring with parted leaves; those that resemble *V. papilionacea* in having uncut leaves always produce offspring with uncut leaves; while those

that have the compromise leaf reproduce plants with three forms of leaf incision, as did the original hybrid. Also in the relative *number* of these forms there is an approximation to the Mendelian ratio 1 : 2 : 1. In the above 26 plants (broods 236 and 468), whose forms were verified by their offspring, there are 9 *A*'s, 11 *Aa*'s, 6 *a*'s, the theoretical ratio being:  $6\frac{1}{2}$  *A*'s, 13 *Aa*'s,  $6\frac{1}{2}$  *a*'s. In the 169 offspring of *Aa* plants, given above for the third and fourth generations, there are 44 *A*'s, 84 *Aa*'s, 41 *a*'s, the theoretical ratio being:  $42\frac{1}{4}$  *A*'s,  $84\frac{1}{2}$  *Aa*'s,  $42\frac{1}{4}$  *a*'s. Here we find, as usual, that the larger the number of individuals the closer the normal ratio is realized.

But besides general conformity there are also departures from the strict Mendelian law. For one thing the hybrid or intermediate leaf varies in different individuals, inclining now more to the form of the one parent species and now more to the form of the other. Also the reversionary forms, designated as *A* and *a*, are rarely complete reversions. The *A* plants, though stable in producing like parted leaves in succeeding generations, do not have leaves as *deeply* parted as in *V. pedatifida*; and the *a* plants, though plainly uncut and stable, usually have teeth noticeably longer than in normal *V. papilionacea*, sometimes even pectinate. (PLATE 15, FIG. *a*.)

Another cause often conspires to increase these differences in leaf pattern: the presence of minor hybrid characters that independently adjust their special conflicts of hybridity. For example, the leaf of *V. pedatifida* is usually truncate or even cuneate at the base, that of *V. papilionacea* usually cordate. A hybrid offspring may inherit the broad truncate base of the former with the uncut margin of the latter. Sometimes in the hybrid leaf the lobes are entire, and obtuse at the tip; sometimes, as in the normal leaf of *V. pedatifida*, the lobes are again cleft or toothed on the outer margin, and acute at the tip.

In these various ways there has arisen in the numerous progeny of the hybrid under discussion a considerable diversity of foliage, such as would present insoluble difficulties to a taxonomic student, who did not know that these diverse forms all came from one individual, by close-fertilized reproduction, in the short period of three or four years. The extreme differences are such as would

warrant the making of several distinct species, according to the hasty methods of ordinary practice.

The hybrid *V. papilionacea*  $\times$  *pedatifida* seems not to be rare in the Middle West. I cite a few interesting examples: *M. A. Castleton* 25, Vinita, Okla., April 18, 1891; distributed as "*V. palmata*."\* From the United States National Herbarium in 1911 was distributed with printed ticket: "*Viola Bernardi* Greene, Freeport, Ill., *Charles F. Johnson*, May 15, 1899; determined by Dr. E. L. Greene and Philip Dowell." The plant is quite the same as the hybrid under discussion from Yorkville, Ill., and seems to represent Dr. Greene's present conception of his species. *V. indivisa* Greene is also a derivative form of this hybrid; the "type" from Prairie Junction, Minn., *E. L. Greene* coll., July 7, 1898 (*Pittonia* 5: 124. *pl.* 13. 1903). Also along railway, Naper-ville, Ill., *L. M. Umbach*, May 18, 1897. (Cf. Leaflets 1: 182. 1906.)

## 2. *Viola pedatifida* $\times$ *sagittata* hyb. nov.

Plant becoming caespitose, the rootstock dividing into several erect branches; leaves that develop after petaliferous flowering finely pubescent especially beneath and on the upper portion of the petiole, the blades subcordate-ovate in outline (the width about  $\frac{2}{3}$  the length), cleft into 6-8 oblong-linear lateral lobes and a broad slightly toothed terminal lobe, the leaves of late summer relatively broader; petals violet, the three lower villous; apetalous flowers and fruit on erect peduncles as long as the petioles; auricles of sepals long and divergent; capsules green, 6-10 mm. long, often quite infertile; seeds intermediate to those of the two parent species in size and color; offspring much unlike each other in foliage, but blades always incised or coarsely toothed toward the base. (PLATE 16, FIG. 4a.)

This hybrid first attracted my attention in a parcel of violet specimens collected in central Illinois by Mr. V. H. Chase, and sent me in November 1907 for determination. It was found in undisturbed prairie soil along the right of way of the Rock Island and Peoria Railroad, just north of the south boundary of Stark County. At the same place and time were collected *V. pedatifida* and pubescent *V. sagittata*, the three plants bearing the consecutive numbers 1356-7-8. The anomalous plant impressed me as

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\* Regarded as *V. viarum* by Mr. Pollard, and apparently the basis for accrediting this species to Ind. Terr. in Britton's Manual, p. 636. 1905.

distinct from *V. pedatifida*  $\times$  *sororia*, discussed below, and as a cross between the two species with which it grew. Mr. Chase, to whom I appealed for living plants, found that the station had been recently burned over; but the following May he discovered another colony along the railway a half mile farther south (*V. H. Chase 1619*). The stocky specimen sent was easily divided, and six or eight vigorous plants were obtained during the season of 1908. Mr. Chase reported that the pubescent *V. sagittata* "was very abundant, thousands of plants cover the ground with a blue carpet, mostly where the land was a little low and damp. *V. pedatifida* seemed to prefer rather drier ground. The hybrid was invariably with *V. pedatifida*, on fairly dry soil; and *V. sagittata* was never more than a few rods away."

During the season of 1909 I grew nineteen offspring of *Chase 1619*, and they gave abundant evidence as to the taxonomic status of the mother plant. Leaves of nine of these offspring are figured in PLATE 16 and indicate something of the marked diversity of form resulting from the combination, in the leaf of the original hybrid, of at least four pairs of opposed characters,\* that blend or segregate, independently and variously, in the several offspring.

### 3. *Viola pedatifida* $\times$ *sororia* hyb. nov.

Becoming cespitose with multicapital caudex; leaves that expand at petaliferous flowering 9-13-cleft, the lateral lobes broadly linear, usually with one or two coarse teeth on the outer edge toward the apex, the middle lobe much broader and incised on either side, the upper face somewhat hirtellous, the lower surface and the petioles villous; the leaves of summer larger and less deeply cleft; apetalous flowers on rather short, erect or ascending peduncles; the capsules somewhat blotched with purple, bearing 5-20 brown seeds 2 mm. long; offspring markedly dissimilar. Not rare on prairies of the Middle West. (PLATE 17.)

I am greatly indebted to the kindness and skill of Mr. Chase for the abundant and excellent material used in the study of this hybrid. Collectors in this region know that the native flora of the open prairies is now largely restricted to untilled strips of land

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| * These are:    | <i>V. pedatifida</i>         | <i>V. sagittata</i>      |
|-----------------|------------------------------|--------------------------|
| 1. Outline      | broadly flabelliform         | lanceolate               |
| 2. Form of base | truncate or cuneate          | cordate or subcordate    |
| 3. Incision     | 2-3-ternately dissected      | coarsely toothed at base |
| 4. Pubescence   | margins and veins hirtellous | finely pubescent         |

along the borders of railways. On May 16, 1909, Mr. Chase, whose bicycle was adjusted to run on rails, traversed in 5 hours the 24 miles between his home at Wady Petra and the town of Galva. In order to make the return by train, he says, "I could not stop to *hunt* along the way; but whenever I saw a cut-leaved violet that was not *V. pedatifida* I stopped for it." The twelve numbers of living plants collected on this trip reached me safely, and all have flourished in the Vermont garden.

The status of hybrid plants in the wild is well shown by a detailed study of these specimens and of their offspring; for all but two sterile plants have been reproduced by seed. The main points regarding them, that have a bearing on the present problem of hybridism, are presented in the following tabular synopsis (TABLE II):

TABLE II  
VIOLET PLANTS COLLECTED BY V. H. CHASE IN CENTRAL ILLINOIS, MAY 16, 1909

|                            | Chase's<br>herb. no. | Leaf characters      |                        | Capsule<br>color     | Seed color                   | Av. no. in<br>one capsule |
|----------------------------|----------------------|----------------------|------------------------|----------------------|------------------------------|---------------------------|
| <i>V. pedatifida</i> Don   | { 1951<br>1956       | <b>A</b><br>(parted) | <b>b</b><br>(glabrous) | <b>c</b><br>(green)  | <b>d</b><br>(buff)           | 70                        |
| <i>V. sororia</i> Willd... | 1291                 | <b>a</b><br>(uncut)  | <b>B</b><br>(villous)  | <b>C</b><br>(purple) | <b>D</b><br>(brown)          | 66                        |
| <i>V. papilionacea</i> Ph. | 1958                 | <b>a</b>             | <b>b</b>               | <b>C</b>             | <b>D</b>                     | 66                        |
|                            | 1950                 | <i>Aa</i>            | <i>b</i>               |                      | sterile                      | 0                         |
| <i>V. papilionacea</i>     | 1952                 | <i>a</i>             | <i>b</i>               | <i>c</i>             | <i>Dd</i>                    | 7                         |
| $\times$ <i>pedatifida</i> | 1949                 | <i>Aa</i>            | <i>b</i>               | <i>Cc</i>            | <i>d</i>                     | 9 $\frac{2}{3}$           |
|                            | 1947                 | <i>Aa</i>            | <i>b</i>               | <i>Cc</i>            | { <i>Dd</i> , or<br><i>d</i> | 5                         |
|                            | 1957                 | <i>Aa</i>            | <i>Bb</i>              |                      | sterile                      | 0                         |
| <i>V. pedatifida</i>       | 1955                 | <i>A</i>             | <i>Bb</i>              | <i>Cc</i>            | <i>Dd</i>                    | 10 $\frac{1}{2}$          |
| $\times$ <i>sororia</i>    | 1953                 | <i>Aa</i>            | <i>Bb</i>              | <i>c</i>             | <i>Dd</i>                    | 7                         |
|                            | 1954                 | <i>Aa</i>            | <i>Bb</i>              | <i>Cc</i>            | <i>Dd</i>                    | 8                         |
|                            | 1948                 | <i>Aa</i>            | <i>Bb</i>              | <i>Cc</i>            | <i>Dd</i>                    | 18                        |

Nos. 1951 and 1956 are *V. pedatifida*; and I have added to the list, though not collected May 16, 1909, *V. sororia*, the other parent of the hybrid under discussion; specimens of this had been previously sent me by Mr. Chase from four stations in his vicinity. No. 1958 is the prairie form of *V. papilionacea*, named *V. pratincola* by Dr. Greene (Pittonia 4: 64. J1 1899). These three are common and widespread species of the Prairie States from Canada to Texas; the first and third reach westward to the mountains of Colorado.

Four of the numbers are the hybrid *V. papilionacea*  $\times$  *peda-*

*tifida*, already discussed in this paper. Of these no. 1950 flowers freely in May with showy flowers, that often appear also in July and August; but apetalous flowers are rare, and neither sort has been found to produce seed. The three others are also nearly sterile, bearing only 5–10 seeds to a capsule; but none of the three turns out to be like the Pollard plant from Yorkville in being a first cross (or  $F_1$ ), the form to be selected as the starting point for experiments on the laws of inheritance in hybrid offspring. No. 1952 has an uncut leaf as in *V. papilionacea* and a green colored capsule as in *V. pedatifida*, both recessive or reversionary characters never found in a first cross. No. 1949, on the other hand, has the hybrid leaf and the hybrid capsule color but the buff seeds of *V. pedatifida* and is therefore another subhybrid. No. 1947 consists of five plants, the seeds of which differ in color, and the leaves of which, though somewhat incised, display at least three unlike patterns; the five plants therefore must be considered the offspring of an earlier hybrid.

The remaining plants of the 1909 collection are equally variant forms but of *V. pedatifida*  $\times$  *sororia*. No. 1957 is of dwarf habit and has the compromise or hybrid leaf; but though vigorous and multiplied by division into eleven plants, it has failed to yield a single seed. No. 1955 (six plants by division) has a leaf more deeply cut than the others, and this style of leaf reappears in all its offspring. In this we see a reversion, far from complete but stable, to the leaf of *V. pedatifida*. No. 1953 (again six plants by division) has the pure green capsules of *V. pedatifida*, as have also its offspring, and so is another subhybrid. But the two remaining numbers, 1954 and 1948, seem to be the desired first product of hybridism, all the four pairs of opposed characters in the double parentage appearing in a compromise form in both numbers. A flowering specimen of 1954 was distributed in my "violets of eastern North America, 1910," no. 121; and in no. 122 are shown two sister offspring, one with the uncut leaves of *V. sororia*, the other with the parted leaves of *V. pedatifida*.\* No.

\* In one of our large herbaria, where the work of mounting is done by novices, these two offspring were considered too unlike to appear on the same sheet. Only the plant with uncut leaves was mounted over ticket 122; while the sister plant with parted leaves was placed on the sheet with no. 121, which indeed it more closely resembled. That two plants so dissimilar should come from one self-fertilized parent has seemed incredible even to certain "botanists."



1948, being unusually fertile for a hybrid, was chosen for the basis of a somewhat detailed study of the reproductive behavior of a tetrahybrid.

During the season of 1910 twenty-one plants were grown from the seeds of *Chase 1948*. In August nearly all bore cleistogamous flowers, which matured several capsules of seeds. These were sown about December 1 in shallow boxes and placed in a cold frame with no protection from the winter weather but a covering of burlap. In the spring of 1911 all but seven of these sowings gave broods of  $F_3$  offspring, containing each 6-18 plants. These have been carefully observed for two seasons and the characters of each plant noted as respects leaf incision, pubescence, color of capsule, and color of seed, four qualities in which the parent species were opposed. In each of these four qualities the plant resembled either *V. pedatifida*, *V. sororia*, or their hybrid; and in most instances the data were at hand, and clear enough, to determine at once this resemblance by inspection. In the case of the sixteen  $F_2$  plants of brood 781, here made use of, the characters were verified by the behavior of their offspring, the reversionary forms always proving stable, the hybrid forms always unstable. The details of this experiment are given in TABLE III, in which the symbols *Aa*, *Bb*, *Cc*, *Dd* denote the blend or hybrid character.

The statements made above regarding the marked diversity of leaf pattern in the offspring of *V. papilionacea*  $\times$  *pedatifida* and the departures from strict Mendelian law are equally true of the analogous hybrid *V. pedatifida*  $\times$  *sororia*. The imperfect reversions in leaf form are shown in PLATE 17, FIG. *A.B*, *A.Bb*, and *A.b*, compared with the leaf of *V. pedatifida* figured above them. But in this hybrid the same phenomena are observable also in the varying colors of capsule and of seed. In all three pairs of characters the stable reversions marked *A*, *C*, and *D* are not complete reversions. The darkest capsule or seed found in the  $F_2$  brood is much lighter than the capsule or seed of *V. sororia*.

It is further to be observed that though the Mendelian law leads us to expect on the average one of each of these reversions in every four offspring, we have here only one of each in the *sixteen* offspring. At the same time the *hybrid* forms are in excess of the

normal average (one half of the whole number); instead of 8 of each we have 10 *Aa*'s, 12 *Cc*'s, and 10 *Dd*'s. And it should be remembered that this statement is not based solely on the appearance of the  $F_2$  plant but on the fact that the reversionary characters, *A*, *C*, *D*, were found to be stable in reproduction; while the hybrid characters were found to be unstable. For example, with the exception of no. 4, which had only two offspring, each of the ten *Aa* plants in brood 781 gave 2-7 plants with uncut leaves.

TABLE III

VIOLA PEDATIFIDA X SORORIA, CHASE 1948, AND ITS OFFSPRING

| Hybrid $F_1$                     | <i>Aa</i> | <i>Bb</i> | <i>Cc</i> | <i>Dd</i> |                              |            |  |
|----------------------------------|-----------|-----------|-----------|-----------|------------------------------|------------|--|
| Forms of sixteen $F_2$ offspring |           |           |           |           | $F_3$ offspring of brood 781 |            |  |
| Brood                            | Foliage   | Capsule   | Seed      | Brood     | Size                         | Exhybrids  |  |
| 781 no. 1                        | <i>a</i>  | <i>B</i>  | <i>Cc</i> | <i>d</i>  | 853                          | 13 plants  | 8 { 5 <i>a.B.C.d</i><br>3 <i>a.B.c.d</i>                     |
| 781 no. 3                        | <i>a</i>  | <i>B</i>  | <i>Cc</i> | <i>d</i>  | 855                          | 10 plants  | 7 { 2 <i>a.B.C.d</i><br>5 <i>a.B.c.d</i>                     |
| 781 no. 4                        | <i>Aa</i> | <i>Bb</i> | <i>Cc</i> | <i>Dd</i> | 856                          | 2 plants   | 0  |
| 781 no. 6                        | <i>A</i>  | <i>Bb</i> | <i>Cc</i> | <i>Dd</i> | 858                          | 16 plants  | 3 { 1 <i>A.B.c.d</i><br>1 <i>A.b.C.d</i><br>1 <i>A.b.c.d</i> |
| 781 no. 7                        | <i>Aa</i> | <i>b</i>  | <i>Cc</i> | <i>Dd</i> | 859                          | 7 plants   | 0  |
| 781 no. 8                        | <i>Aa</i> | <i>B</i>  | <i>C</i>  | <i>d</i>  | 860                          | 6 plants   | 4 { 2 <i>a.B.C.d</i><br>2 <i>A.B.C.d</i>                     |
| 781 no. 9                        | <i>Aa</i> | <i>B</i>  | <i>Cc</i> | <i>D</i>  | 861                          | 16 plants  | 3 { 1 <i>A.B.C.D</i><br>1 <i>A.B.c.D</i><br>1 <i>a.B.c.D</i> |
| 781 no. 10                       | <i>Aa</i> | <i>b</i>  | <i>Cc</i> | <i>Dd</i> | 862                          | 14 plants  | 1 <i>a.b.c.D</i>   |
| 781 no. 11                       | <i>Aa</i> | <i>Bb</i> | <i>c</i>  | <i>Dd</i> | 863                          | 11 plants  | 2 { 1 <i>A.b.c.d</i><br>1 <i>a.b.c.d</i>                     |
| 781 no. 13                       | <i>a</i>  | <i>Bb</i> | <i>Cc</i> | <i>Dd</i> | 865                          | 2 plants   | 0  |
| 781 no. 14                       | <i>a</i>  | <i>B</i>  | <i>c</i>  | <i>Dd</i> | 866                          | 9 plants   | 6 { 3 <i>a.B.c.D</i><br>3 <i>a.B.c.d</i>                     |
| 781 no. 15                       | <i>Aa</i> | <i>Bb</i> | <i>C</i>  | <i>d</i>  | 867                          | 15 plants  | 1 <i>a.B.C.d</i>   |
| 781 no. 16                       | <i>Aa</i> | <i>Bb</i> | <i>Cc</i> | <i>Dd</i> | 868                          | 10 plants  | 0  |
| 781 no. 17                       | <i>Aa</i> | <i>Bb</i> | <i>Cc</i> | <i>d</i>  | 869                          | 18 plants  | 2 { 1 <i>a.B.C.d</i><br>1 <i>a.B.c.d</i>                     |
| 781 no. 19                       | <i>a</i>  | <i>b</i>  | <i>Cc</i> | <i>Dd</i> | 871                          | 8 plants   | 1 <i>a.b.c.d</i>   |
| 781 no. 20                       | <i>Aa</i> | <i>b</i>  | <i>Cc</i> | <i>Dd</i> | 872                          | 14 plants  | 3 { 1 <i>A.b.C.d</i><br>1 <i>A.b.c.d</i><br>1 <i>a.b.c.d</i> |
|                                  |           |           |           |           |                              | 171 plants | 41   |

And not only in the second but also in the third generation of this hybrid the number of plants having the positive character seems to fall short of the Mendelian requirements. This appears if

we note the ratio in which the several hybrid characters in brood 781 segregate in the  $F_3$  offspring:

|  |              |   |                        |
|--|--------------|---|------------------------|
| The 10 <i>Aa</i> plants had 113 offspring: 23 <i>A</i> 's, 54 <i>Aa</i> 's, 36 <i>a</i> 's | } ratio in % | { | 20:48:32               |
| The 7 <i>Bb</i> plants had 74 offspring: 14 <i>B</i> 's, 35 <i>Bb</i> 's, 25 <i>b</i> 's   |              |   | 19:47:34               |
| The 12 <i>Cc</i> plants had 130 offspring: 23 <i>C</i> 's, 67 <i>Cc</i> 's, 40 <i>c</i> 's |              |   | 18:51:31               |
| The 10 <i>Dd</i> plants had 93 offspring: 18 <i>D</i> 's, 44 <i>Dd</i> 's, 36 <i>d</i> 's  |              |   | 14:47:39               |
| Total 410  | 73           |   | normal ratio: 25:50:25 |

Combining these results, we find in 410 instances of the reproduction of a hybrid character, that instead of  $102\frac{1}{2}$  reversions to the positive character there are only 73; instead of 25 per cent, only 18.

However, the determination of the characters in these 171  $F_3$  offspring rests only upon their appearance, having not been as yet verified by observing the behavior of the  $F_4$  offspring. Of this generation 45-50 broods are hoped for by another season from seed already sown. But we seem to be already justified in the suspicion that in a species-hybrid as complex as the one under experiment, where the opposed characters of the parents appear in a blend or intermediate form, this form may acquire a certain degree of fixity, whereby the reversions to the positive type in a pair of opposed characters are less complete and less frequent than in normal Mendelian segregation and the reversions to the negative type more frequent. If we might assume that the gametes holding the positive character were more or less impure, while the gametes holding the negative character were pure, the situation would be fairly well accounted for.

In the great diversity of forms displayed in the 171  $F_3$  offspring the most interesting group are the 41 exhybrids, in which all of the four characters under study are reversionary and constant. Among these we find three plants in which the four characters of *V. pedatifida*, *A.b.c.d*, reappear, one plant in each of the broods 858, 863, and 872. What may be called a form of *V. pedatifida* with uncut leaves, *a.b.c.d*, is found once in each of the broods 863, 871, 872. A pubescent *V. pedatifida*, *A.B.c.d*, occurs in brood 858. A purple-capsuled *V. pedatifida*, *A.b.C.d*, occurs in both 858 and 872. Similarly, we have a cut-leaved *V. sororia*, *A.B.C.D*, in brood 861; a green-capsuled *V. sororia*, *a.B.c.D*, once in brood 861 and three times in brood 866; and a buff-seeded *V. sororia*, *a.B.C.d*, in broods 853, 855, 860, 867, and 869, eleven plants in all. In short, all but five of the sixteen possible combi-

nations in fours, of these eight pure elementary characters, are to be found in these 41 plants.

As showing how a hybrid tends in successive generations to eliminate its hybrid characters, ever becoming simpler and finally pure, we note that starting with the  $F_1$  plants, necessarily hybrid in all the opposed characters of the two parent species, we have in the next generation only two such hybrids, and in the 171 plants of the 3d generation, none; indeed, the law of probability calls here for only one in every 256 offspring.

My first recognition of *V. pedatifida*  $\times$  *sororia* was in a package of living plants sent May 22, 1907, by Dr. H. V. Ogden of Milwaukee, collected at Upper Nemahbin Lake, Wis., growing with both parents, and considered by him as "doubtless a hybrid." The same thing, however, had been sent me some three years earlier by Dr. Greene as a specimen of his *V. Bernardi*, collected by himself at Dixon, Ill., June 18, 1898. In Leaflets 1: 184. Ja 1906, the plant is transferred to *V. perpensa*, then first described. I have recently examined the three other specimens there cited and regard them all as forms of *V. pedatifida*  $\times$  *sororia*.\* Also *V. fallacissima* Greene, Leaflets 1: 185. Ja 1906, is another form of the same hybrid from western Missouri—*Bush 141*, Lee's Summit, Mo., July 8, 1899. Other specimens are: *E. J. Palmer 3345 and 3393*, Webb City, Mo., April 19 and May 5, 1911; *Mary O. Pollard 6*, Yorkville, Ill., May 16, 1909; *L. M. Umbach*, prairies, Clarendon Hills, Ill., June 21, 1899—distributed in 1911 from United States National Herbarium as "*V. palmata*."

#### 4. *Viola nephrophylla* $\times$ *pedatifida* hyb. nov.

*V. Wilmattae* Pollard, Proc. Biol. Soc. Wash. 15: 178. Au 1902†

Foliage much as in *V. papilionacea*  $\times$  *pedatifida*, nearly glabrous, palmatifid with several narrow lateral lobes; corolla "deep violet, 2 cm. broad"; petals markedly villous and sepals with slightly scarious margins, as in *V. nephrophylla*.

It has not been practicable to secure living plants for cultures. But the alleged parent species were both growing in the cañon,

\* I therefore wish to correct my statement in Bull. Torrey Club 37: 584. 1910 that *V. perpensa* Greene is the western form of *V. palmata*—a too hasty inference from the fact that a *V. palmata* specimen in my herbarium from Aurora, Ill., was once named *V. Bernardi* by Mr. C. L. Pollard.

† The type is 404,924 United States National Herbarium, *Mrs. Wilmatte P. Cockerell*, Sapello Cañon (c. 8000 ft. alt.), Beulah, New Mex., May 5, 1901.

and the status of the plant is strikingly analogous to that of numbers 1 and 3 above described. The supposed hybrid has been recently again collected, by Mr. Paul C. Standley.\* The leaves in his specimens are cut about halfway to the midrib; but on the same sheet are two detached leaves parted as in *V. pedatifida*, indicating that this species grew with the anomalous plant.

MIDDLEBURY, VERMONT

### Explanation of plates

#### PLATE 1

Figures  $\frac{1}{2}$  natural size

- Aa. Viola papilionacea*  $\times$  *pedatifida* Brainerd, transplanted, May 1905, from Yorkville, Ill., Mary O. Pollard coll.; ex horto Middlebury, Vt., May 14, 1910. No. 109 Brainerd's violets of eastern No. Am., 1910.
- A. F*<sub>4</sub> offspring of *Aa*, having stable leaf pattern resembling that of *V. pedatifida*; ex horto (brood 612) Middlebury, Vt., June 2, 1912.
- a. F*<sub>2</sub> offspring of *Aa*, having stable leaf pattern resembling that of *V. papilionacea*; ex horto (brood 236 plant 6) Middlebury, Vt., June 3, 1909.

#### PLATE 2

Figures  $\frac{1}{2}$  natural size

- A. Leaf of Viola pedatifida* Don, south of Wady Petra, Stark Co., Ill., V. H. Chase 1356, May 26, 1907.
- a. Leaf of pubescent V. sagittata* Ait., south of Wady Petra, Ill., V. H. Chase 1524, July 28, 1907.
- Aa. Viola pedatifida*  $\times$  *sagittata* Brainerd, transplanted, May 3, 1908, from along railway  $1\frac{1}{4}$  miles south of Wady Petra, Ill., V. H. Chase 1619; ex horto Middlebury, Vt., Sept. 7, 1909.
- 1-13. Characteristic leaves of nine *F*<sub>2</sub> offspring of above hybrid; ex horto (brood 630) October 1909.

#### PLATE 3

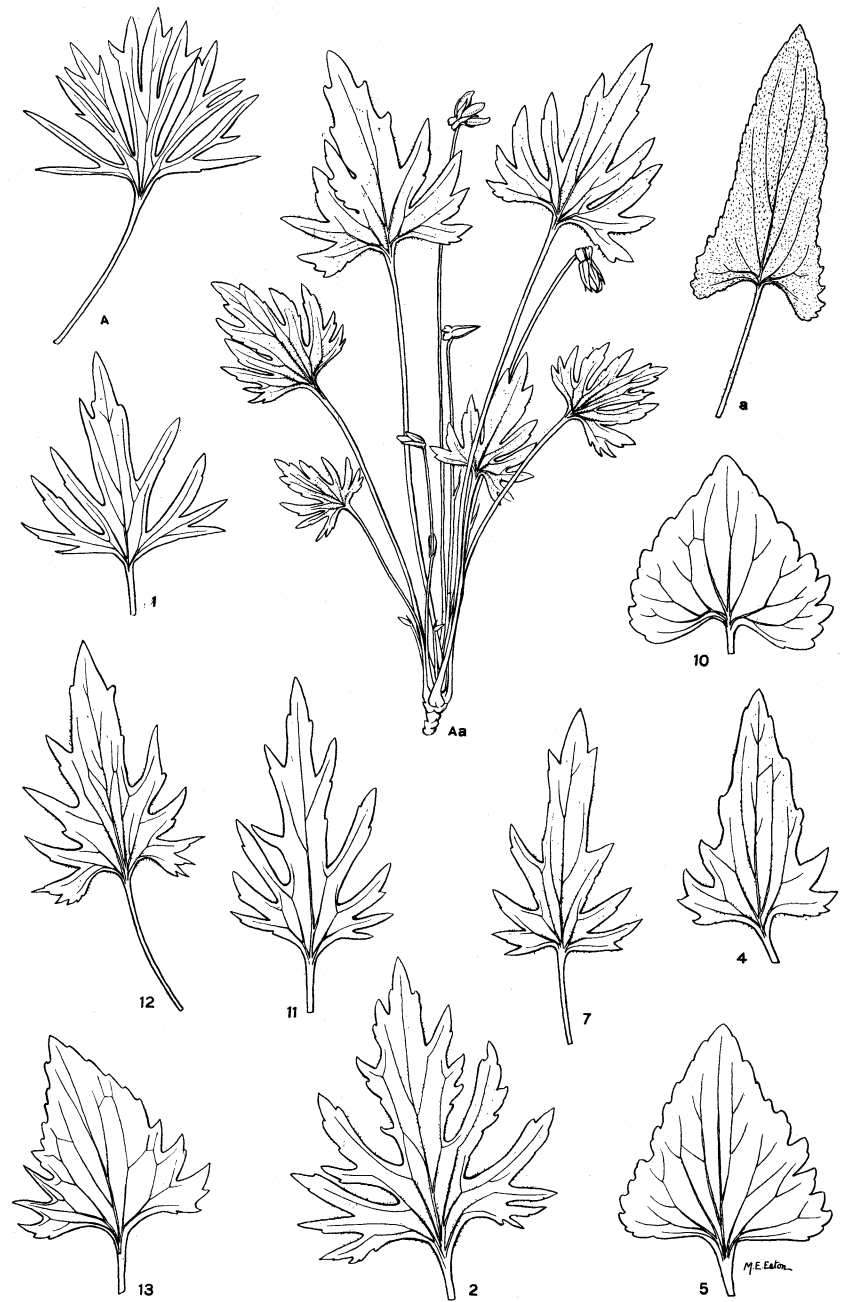
Figures  $\frac{1}{2}$  natural size

- A leaf of *Viola pedatifida* Don, transplanted, May 1909, from near Galva, Ill., V. H. Chase 1951; ex horto (brood 851) Oct. 3, 1911.
- A leaf of *V. sororia* Willd., transplanted, May 1909, from Yorkville, Ill., Mary O. Pollard coll.; ex horto (brood 707) Aug. 31, 1910.
- Hybrid leaf of *V. pedatifida*  $\times$  *sororia* Brainerd, transplanted, May 1909, from along railway, Stark Co., Ill., V. H. Chase 1948; ex horto Aug. 31, 1909.
- A.B.—a.b.* Characteristic leaves of nine offspring of this hybrid, viz:
- A.B, F*<sub>3</sub>, plant 1 of brood 861, stable as to pubescent palmatifid leaf.
- Aa.B, F*<sub>2</sub>, plant 9 of brood 781, stable as to pubescent leaf only.
- a.B, F*<sub>2</sub>, plant 14 of brood 781, stable as to pubescent uncut leaf.
- A.Bb, F*<sub>3</sub>, plant 8 of brood 868, stable as to palmatifid leaf only.
- Aa.Bb, F*<sub>2</sub>, plant 17 of brood 781, hybrid in both pubescence and form of leaf.
- a.Bb, F*<sub>3</sub>, plant 8 of brood 867, stable as to uncut leaf only.
- A.b, F*<sub>4</sub>, plant 9 of brood 995, stable as to glabrous palmatifid leaf.
- Aa.b, F*<sub>2</sub>, plant 7 of brood 781, stable as to glabrous leaf only.
- a.b, F*<sub>4</sub>, plant 0 of brood 998, stable as to glabrous uncut leaf.

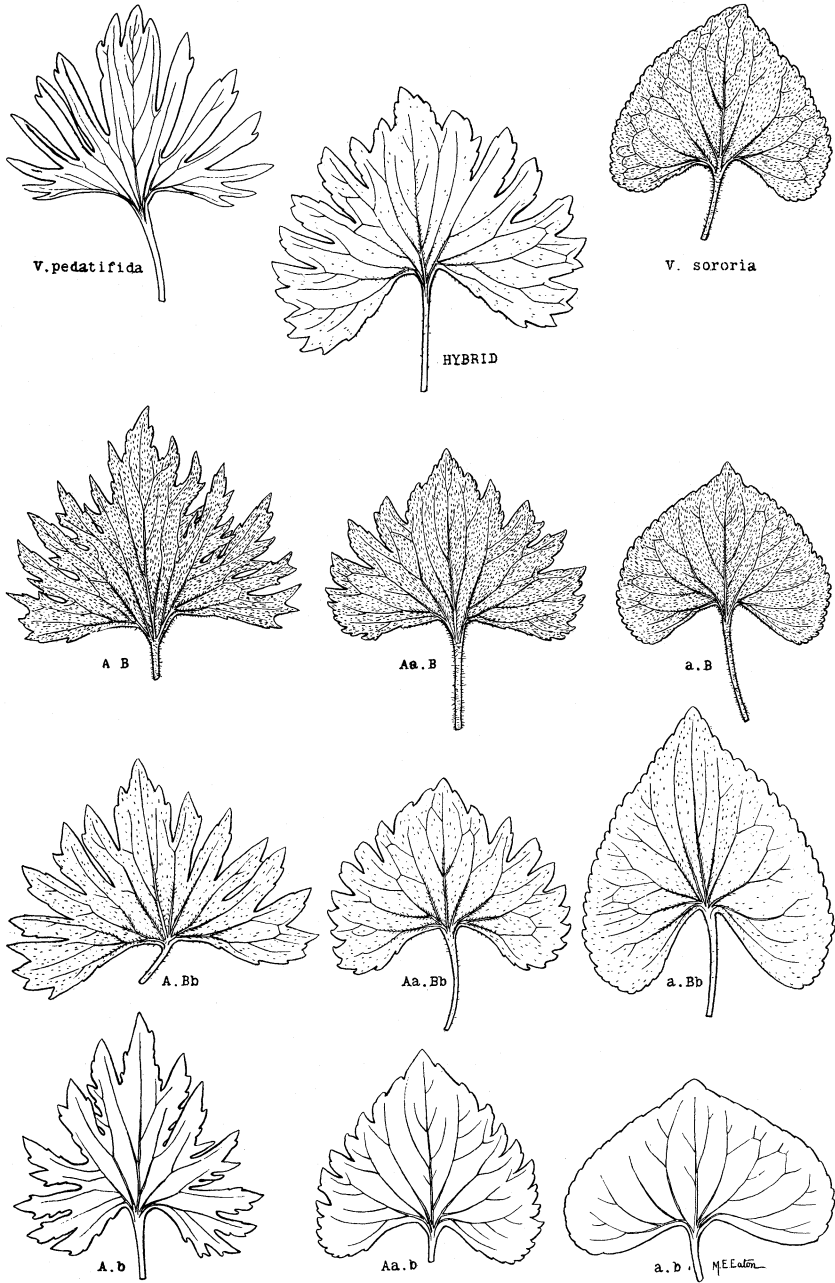
\* United States National Herbarium, Standley 6072, near the Sierra Grande 2100-2925 m. alt.), Union Co., New Mex., June 18, 1911.



*VIOLA PAPILIONACEA* X *PEDATIFIDA* AND TWO OF ITS SEGREGATE OFFSPRING



VIOLA PEDATIFIDA X SAGITTATA AND LEAVES OF ITS PARENTS AND OF NINE OFFSPRING



LEAVES OF VIOLA PEDATIFIDA X SORORIA, OF ITS PARENTS, AND OF NINE OFFSPRING